THE RHYNCHOSAUR *HOWESIA BROWNI* FROM THE LOWER TRIASSIC OF SOUTH AFRICA

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ABSTRACT. *Howesia browni* is a rhynchosaur (Reptilia: Archosauromorpha) known from a single locality in the *Cynognathus* Assemblage Zone (Beaufort Group: Burgersdorp Formation) near the town of Aliwal North, Eastern Cape Province, South Africa. *Howesia* is diagnosed by the following autapomorphies: (1) multiple rows of small, conical teeth on medially expanded maxillaries that lack longitudinal, occlusal grooves; (2) multiple rows of small, conical teeth on dentaries; (3) a broad ventral process of the squamosal that does not extend below the middle of the lower temporal fenestra; (4) a medial shelf on the quadrate ramus of the pterygoid; (5) contact between the ectopterygoid and jugal reduced to less than half of the distal expansion of the ectopterygoid; (6) deep pockets on the neural arches of the posterior dorsals and sacrals; and (7) posteriorly inclined and tall proximal caudal neural spines. A preliminary phylogenetic analysis demonstrates that Rhynchosauria can be rediagnosed by seven synapomorphies: (1) a beak-shaped premaxilla; (2) a single, median external naris; (3) contact between the premaxilla and prefrontal; (4) depression on the dorsal surface of the frontal; (5) depression on the dorsal surface of the postfrontal; (6) fused parietals; and (7) flat occlusion. *Howesia* is the probable sister taxon to the clade of *Rhynchosaurus*, *Stenaulorhynchus*, *Scaphonyx* and *Hyperodapedon*.

RHYNCHOSAURS are a clade of herbivorous diapsid reptiles of the Triassic Period (245–208 Ma) ranging in bodily length from less than 1 m to approximately 2 m. Rhynchosaur fossils have been found on every major land mass with the exceptions of Antarctica and Australasia. Their abundance in the Middle and Late Triassic indicates that they were a common component of many faunas (Benton 1983a; Benton and Walker 1985; Holtz and Barberena 1994). Detailed descriptions (e.g. Huene 1938; Chatterjee 1974; Benton 1983b, 1990) of the Middle and Late Triassic genera have provided significant data for phylogenetic analyses (e.g. Gauthier 1984; Benton 1985; Evans 1988; Laurin 1991) of Permian and Triassic diapsids. The diet of rhynchosaurs has been hypothesized to be plants (Huene 1939a; Sill 1971; Benton 1983b, 1984) or molluscs (Chatterjee 1974, 1980), but the morphology of rhynchosaurian teeth is different from that of extant vertebrates that eat molluscs, and the unique precision-shear bite of rhynchosaurs is an unlikely method for breaking apart hard-shelled invertebrates (Benton 1983b, 1984). The long, beak-shaped premaxillae probably gathered a variety of plants such as seed-ferns, conifers, cycads, ginkgos, and ferns, which were cut, but not masticated, by the powerful jaws. Roots and tubers were perhaps dug using the hind limb and its large claws.

Far less is known about Early Triassic rhynchosaurs. Three species, *Howesia browni* Broom, 1905, *Mesosuchus browni* Watson, 1912a, and *Noteosuchus colletti* (Watson, 1912b), that are restricted presently to the Middle and Upper Beaufort Group of South Africa, furnish the only information on the early stages of rhynchosaurian phylogeny (Broom 1906, 1913, 1925; Haughton 1921, 1924; Malan 1963; Carroll 1976). The importance of these genera lies in their basal position within Rhynchosauria according to stratophenetic phylogenies (Chatterjee 1969, 1974, 1980) and cladistic analyses (Benton 1987, 1990). Incorporation of basal taxa of a group (plesiomorphic sister taxa) in a cladistic analysis can alter tree topologies and ideas of character evolution, which will in turn affect phylogenetically dependent hypotheses (Donoghue *et al.* 1989). Cladistic studies of diapsids (e.g. Benton 1985; Evans 1988; Laurin 1991) have supported prior arguments (Hughes 1968; Carroll 1976; Brinkman 1981; Benton 1983b) that rhynchosaurs should not be grouped with

rhynchocephalian sphenodontids such as the extant *Sphenodon* in Lepidosauria, as believed traditionally (e.g. Nopsca 1928; Romer 1956; Kuhn 1969). Instead, these studies agree that rhynchosaurs are early members of Archosauromorpha, a clade whose extant members are crocodiles and birds. Thus, data from the South African rhynchosaurs have the potential to modify the composition and diagnosis of Rhynchosauria and alter our conception of the interrelationships of basal archosauromorphs.

Beyond the initial cursory descriptions by Broom (1905, 1906), only selected aspects of the anatomy of *Howesia browni* have appeared in the literature (Haughton 1924; Malan 1963; Carroll 1976). Additional preparation of the three known specimens of *Howesia* has revealed considerable new data, especially of the skull, allowing for the first time a detailed comparison with the other two South African rhynchosaurs and other archosauromorphs. Comparisons with *Mesosuchus* are based upon personal observations of all known material that will be the subject of a forthcoming publication. The Early Triassic rhynchosaur *Howesia browni* is redescribed here, and a preliminary phylogenetic analysis is presented for Rhynchosauria.

Institutional abbreviations are: SAM, South African Museum, Cape Town; BP/1/, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa.

SYSTEMATIC PALAEONTOLOGY

REPTILIA Laurenti, 1768
DIAPSIDA Osborn, 1903
RHYNCHOSAURIA Osborn, 1903

Genus HOWESIA Broom, 1905

Type species. Howesia browni Broom, 1905

Diagnosis. As for the only species.

Howesia browni Broom, 1905

Text-figures 1–7

Revised diagnosis. Small (total length less than 1 m) rhynchosaurian diapsid that is distinguished from all other rhynchosaurs by the following autapomorphic characters: multiple rows of small, conical teeth with ankylothecodont implantation in medially expanded maxillaries that lack longitudinal, occlusal grooves; multiple rows of numerous conical teeth on the dentaries; broad ventral process of squamosal that does not extend below middle of lower temporal fenestra; horizontal shelf on medial side of quadrate ramus of pterygoid; contact between ectopterygoid and jugal reduced to less than half of the length of the distal expansion of the ectopterygoid; deep pockets on neural arches of posterior dorsal and sacral vertebrae; and tall, posteriorly inclined neural spines of proximal caudal vertebrae.

Holotype. SAM 5884 (specimen A), a partial skull with palate and incomplete lower jaws.

Hypodigm. SAM 5885 (specimen B), a dorsoventrally crushed skull with a partial palate, braincase, and atlas-axis complex; and SAM 5886 (specimen C), a partial, articulated postcranium consisting of the posterior four dorsal vertebrae, sacrals, first dozen caudals, incomplete pelvic girdles, a partial left hind limb, and a complete right tarsus described by Carroll (1976).

Locality and horizon. Precise location is unknown, but near the town of Aliwal North, Eastern Cape Province, South Africa (Broom 1905, 1906). Exposures near Aliwal North are part of the *Cynognathus* Assemblage Zone (Kitching in press) which coincides with the upper two-thirds of the Burgersdorp Formation (Tarkastad Subgroup, Beaufort Group; Keyser and Smith 1979). Age is probably late Early Triassic (Scythian).

Preparation. Preparation was undertaken with a pneumatic tool and a pin vice with a tungsten needle. Specimens were impregnated with Glyptal resin. Plaster of paris was used to reinforce portions of SAM 5884 and to embed SAM 5885 to allow preparation of both sides. Latex rubber casts were made of the right dentary teeth and left jugal of SAM 5884 which are preserved as impressions in the matrix.

DESCRIPTION

Skull

Restoration of the skull. Only two prior attempts (Broom 1906; Huene 1939*b*) have been made to reconstruct the skull of *Howesia*. Both reconstructions depicted a skull similar in its proportions to that of *Sphenodon* and with a complete lower temporal bar. Broom (1906) restored *Howesia* with a blunt snout and laterally placed external nares whereas Huene (1939*b*) argued that *Howesia* should have a downturned premaxilla as in *Sphenodon*, and positioned a single external naris dorsally along the premaxilla-nasal suture.
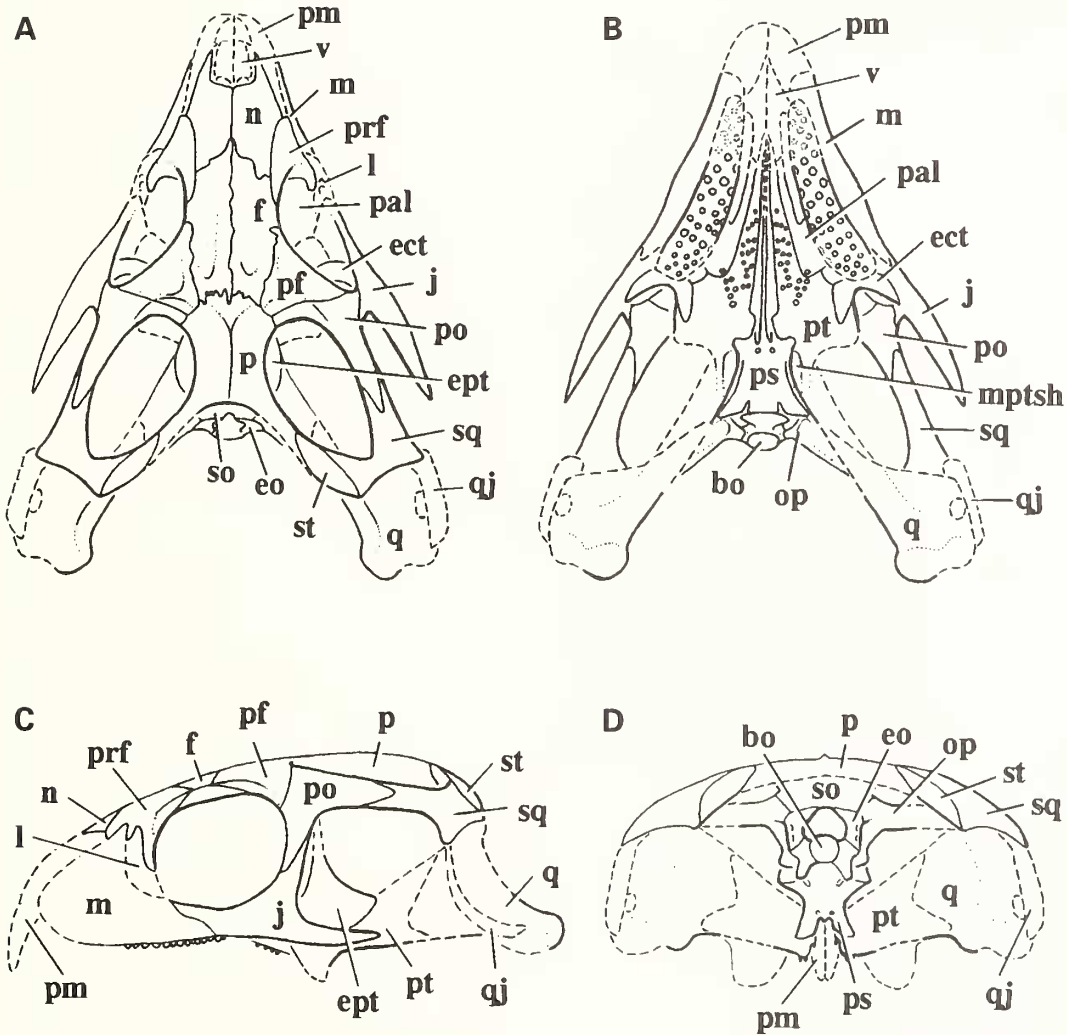
TEXT-FIG. 1. Restoration of the skull of *Howesia browni* Broom, 1905; Early Triassic; South Africa. A, dorsal view. B, ventral view. C, left lateral view. D, occipital view. Scale bar represents 20 mm.

Based upon the new cranial data described herein, *Howesia* has a broad skull that tapers gradually to the premaxillae (Text-fig. 1). A downturned, edentulous premaxillary beak is restored, because this morphology is correlated with broad maxillary tooth plates in other rhynchosaurs. The lower temporal bar is incomplete and the lower temporal fenestra is much larger than restored by Broom (1906) and Huene (1939*b*). The preserved portion of the quadrate suggests that it is a robust element that placed the craniomandibular joint significantly posterior to the occipital condyle in contrast with earlier restorations. A slender quadratojugal is restored, in agreement with *Mesosuchus*, but its existence in *Howesia* is, at present, purely conjectural.

Dermal bones of skull. Premaxillae are absent in SAM 5884 and 5885; hence, it is unknown if *Howesia* has a downturned premaxilla, common to all other rhynchosaurs, or premaxillary teeth, as in *Mesosuchus*. Nonetheless, the construction of the nasals, as discussed below, does suggest that the shape of the premaxillae is similar to that of *Mesosuchus* (Haughton 1924).
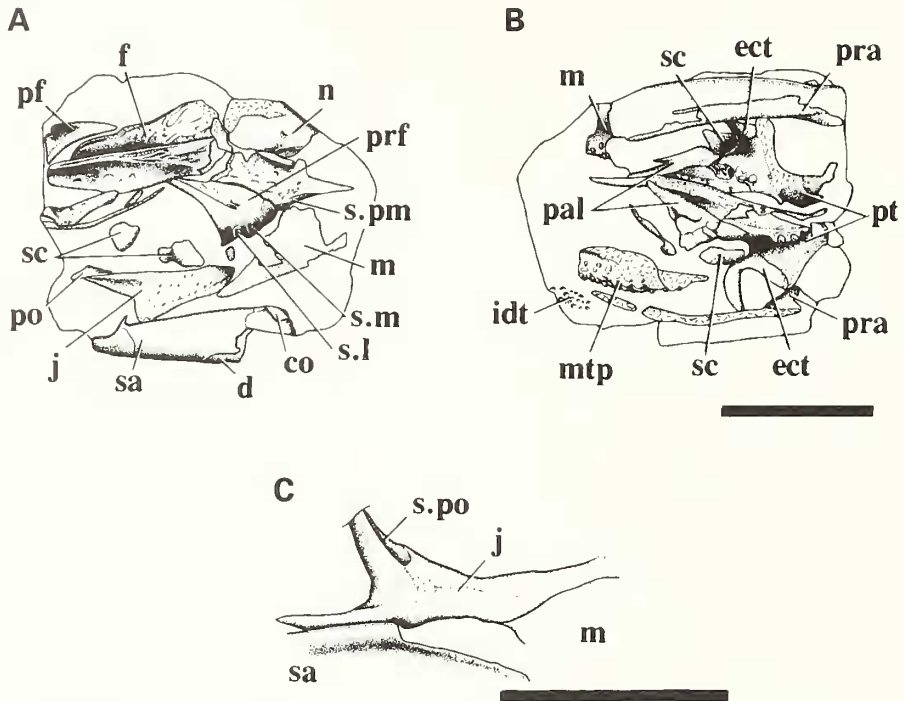
TEXT-FIG. 2. *Howesia browni* Broom, 1905; holotype, SAM 5884; Early Triassic; South Africa. A, dorsolateral view. B, ventromedial view. C, internal view of left jugal, surangular, and maxilla. Scale bars represent 20 mm.

A complete right nasal and a partial left nasal are exposed on the type specimen (Text-fig. 2A). Few differences exist between the nasals of *Howesia* and *Mesosuchus*, and it is clear that *Howesia* has a single, median external naris in agreement with other rhynchosaurs. A sharp ridge along the lateral edge of the nasal demarcates the dorsal surface from a laterally extensive articular region for the posterodorsal process of the premaxilla, as in *Mesosuchus*. The sutural surface for the premaxilla extends to the prefrontal indicating contact between these elements. *Howesia* lacks processes of the nasals like those which project into the external naris in *Mesosuchus* (Haughton 1924) and meet premaxillary processes in more plesiomorphic diapsids. There is a scattering of small pits near the suture with the premaxilla and external naris and a few shallow, longitudinal grooves.

The right maxilla on the type specimen consists of the thin and poorly preserved lateral face and a portion of the medially expanded tooth plate. Owing to the poor preservation, no sculpturing is present.

Three prominent sutural regions for neighbouring bones are visible on the lateral side of the prefrontal: a smaller, posterior, and deeply recessed facet for a narrow dorsal process of the lacrimal; a broader, shallower surface for the maxilla; and a small, anterior facet for the posterodorsal process of the premaxilla. A narrow process of the prefrontal extends along the orbital rim, but does not contact the postfrontal.

Neither skull of *Howesia* has a preserved lacrimal, but its presence is indicated on the type specimen by the articular surface on the lateral side of the prefrontal. Contact between the maxilla and the prefrontal precluded any union between the lacrimal and nasal.

A right jugal (Text-fig. 2A) and an impression of most of the left jugal (Text-fig. 2C) are preserved on the type, and an incomplete left jugal is present on SAM 5885 (Text-fig. 3A). The triradiate jugal consists of an anterior
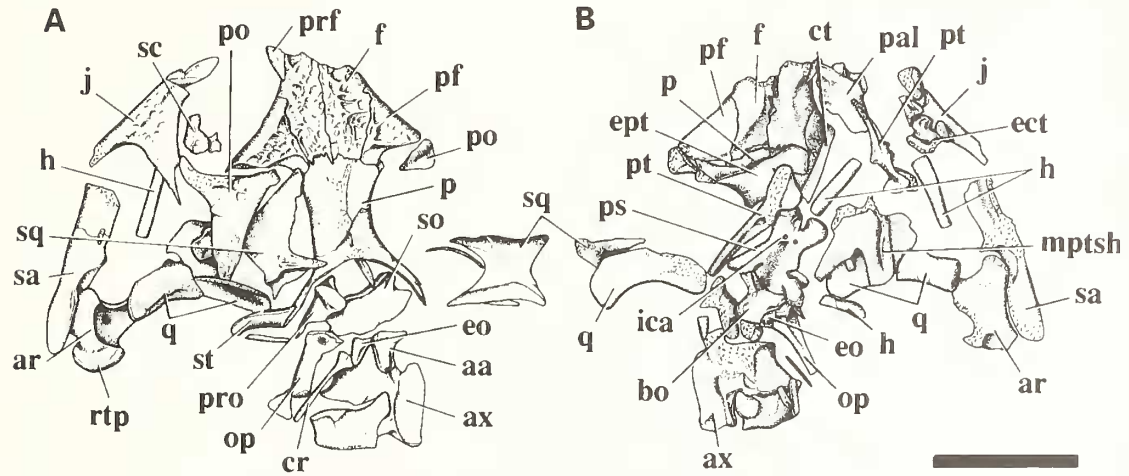
TEXT-FIG. 3. *Howesia browni* Broom, 1905; SAM 5885; Early Triassic; South Africa. A, dorsal view. B, ventral view. Scale bar represents 20 mm.

process that forms the entire ventral orbital rim and is overlapped by the maxilla, a posterodorsal process tapering dorsally along the postorbital, and a posterior process that forms the lower temporal bar. As the completeness of the lower temporal bar in diapsids is a character of phylogenetic significance (Benton 1985; Chatterjee 1986) and it is a point of contention whether or not *Mesosuchus* has a complete lower temporal bar (Haughton 1924; Broom 1925), it is crucial to determine the condition for *Howesia*. Broom (1906) restored *Howesia* with a complete lower temporal bar, arguing that the configuration of the jugal was nearly identical to the jugal of the early reptile *Palaeohatteria* which at that time was thought to be the oldest known diapsid, but recognized later as a synapsid (Williston 1925). He based his claim for a complete temporal bar upon an impression of the left jugal of the type specimen and the incomplete left jugal of SAM 5885. His reconstruction of *Howesia* (Broom 1906, plate XL, figure 1), which appears to be derived largely from SAM 5885, shows, incorrectly, a jugal with a bluntly tipped posterior process that presumably met an anterior process of the quadratojugal. In fact, the left jugal of the type specimen has a complete posterior process that tapers sharply (Text-fig. 2C). In addition, there is no facet on the internal surface of the jugal for the quadratojugal as would appear to be true for other rhynchosaurs with a complete lower temporal bar (Huene 1938; Benton 1983b, 1990). Therefore, the jugal of *Howesia* does not contact the quadratojugal, and the lower temporal bar is incomplete.

Frontals have a longitudinal depression on their dorsal sides that increases in depth posteriorly to a maximum next to the frontal–postfrontal contact. Sculpturing consists of circular to oval pits that are much larger and deeper on SAM 5885.

Postfrontals are distinguished by a marked depression on their dorsal sides situated at the posteromedial corner next to the contact between the frontal, parietal, and postorbital. This depression lessens in depth anterolaterally to the thickened orbital rim. A cluster of shallow pits is present in the postfrontal depression

of the type specimen; those on SAM 5885 are more pronounced and include broad grooves that are oriented towards the orbital rim. Each postfrontal of SAM 5885 has a dorsally facing, smooth region next to the parietal that is continuous with the ventrolateral flange of the parietal, demonstrating that the postfrontal entered the upper temporal fenestra.

Only the left postorbital of SAM 5885 (Text-fig. 3A) is virtually complete. A gently tapering anterodorsal process of the postorbital contacts the parietal and the equally constricted ventral process fits in to a long recess on the dorsal process of the jugal (Text-fig. 2C). The posterodorsal process is broader than the other two processes and tapers sharply. Faint, longitudinal striations on the posterodorsal process and some small pits on the anterodorsal process comprise the sculpturing for this element.

Parietals of SAM 5885 are fused along their common, midline suture which is raised slightly to form a low, but sharply defined ridge. Anteriorly, the ridge divides and extends to the parietal-frontal suture. An apparently rudimentary pineal foramen (Broom 1906) is merely a deep concavity that does not penetrate the parietals. Laterally, the parietals expand into ventrolateral flanges which apparently provided increased surface area for attachment of mandibular adductor muscles. Along the occipital rim, the parietals are drawn laterally and posteriorly into tall, anteroposteriorly narrow wings.

No mention of an element lateral to the parietal wings, other than the squamosal, appeared in Broom's (1906) account of *Howesia*. Haughton (1924) identified supratemporals (tabulars of Broom 1925) in both *Howesia* and *Mesosuchus*, but it is clear, upon comparison of his drawing of SAM 5885 with the specimen, that the elements labelled as supratemporal and squamosal are actually the squamosal and pterygoid portion of the quadrate, respectively. In fact, the genuine supratemporal is not shown in his drawing because it had not been exposed. Only the left supratemporal of SAM 5885 is exposed and is very similar to the supratemporal of *Mesosuchus*. Each is a tall, thin bone that fits into an elongate, occipitally facing concavity on the squamosal and is overlapped marginally by the parietal wing. Consequently, exposure of the supratemporal is primarily occipital and limited to the posterolateral corner of the skull.

The squamosal of *Howesia* (Text-fig. 3A) is a broad, tetraradiate element that forms a significant portion of the borders of the upper and lower temporal fenestrae. The ventral process is broad and tapers abruptly to a blunt tip, and its participation in the rear border of the lower temporal fenestra is restricted to only the upper half. In other basal archosauromorphs, the ventral process is either much narrower and extends to the midpoint of the temporal fenestra (*Prolacerta*: BP/1/2675 and BP/1/471; *Euparkeria*: Ewer 1965) or is more robust and extends below the middle of the temporal fenestra (*Mesosuchus*: Haughton 1924; *Proterosuchus*: Welman in press).

Sclerotic elements. Fragments of extremely thin bone are present in the orbits of SAM 5884 and 5885 and the suborbital fenestrae of SAM 5884 (Text-figs 2–3). These fragments are evidently the remains of sclerotic rings with each element, judging by the size of the larger fragments relative to the orbit, part of a substantial ring of bone. A sclerotic ring in the orbit of a rhynchosaur was first reported in *Hyperodapedon gordoni* (Benton 1983b).

Dermal bones of the palate. Only partial palates remain on SAM 5884 and 5885 (Text-figs 2B, 3B). The pterygoids appear to be united along most of their dorsally expanded medial surfaces, but separate just anterior to the basal articulation. Each palatal ramus of the pterygoids has two narrow fields of large denticles on slightly raised ridges that converge medially at the point of midline pterygoid separation. One field continues anteriorly along the medial edge while the second is directed anterolaterally towards the palatine and the anterior margin of the suborbital fenestra. The transverse flanges of SAM 5884 and 5885 are damaged and it is unknown if teeth were present. The basal process of SAM 5885 is a robust, dorsomedially oriented projection with an articular surface of the basipterygoid process that faces posterodorsally and slightly medially. A distinctive horizontal shelf that arises from the medial surface of the vertical quadrate ramus (Text-fig. 3B) is autapomorphic for *Howesia*.

The ectopterygoid of *Howesia* is an elongate element sutured along the lateral side of the pterygoid (Text-fig. 2B). Ectopterygoid and pterygoid are joined by a complex interlocking suture in which, in ventral view, the pterygoid overlaps the ectopterygoid for the anterior half of the suture and is in turn overlapped by the ectopterygoid for the remainder. *Mesosuchus* has an identically constructed suture between the ectopterygoid and pterygoid, and a similar configuration has been described recently in the archosauriform *Proterosuchus* (Welman in press). The posterior edge of the ectopterygoid does not reach the transverse flange in these three genera. *Prolacerta* is restored with a more abbreviated ectopterygoid (Gow 1975); however, after examination of the specimen (BP/1/2675) which served as the basis for this restoration, it is clear that the ectopterygoid is incomplete and continued posteriorly along the damaged lateral edge of the pterygoid for an uncertain

distance. Ventrally, the pterygoid of *Prolacerta* does overlap the preserved anterior portion of the ectopterygoid, and the possibility that *Prolacerta* shares a similar sutural pattern with the aforementioned archosauromorphs cannot be ruled out. The ectopterygoid has a lunate process that contacted the jugal, but apparently not the maxilla. In contrast with the more robust contact between the ectopterygoid and jugal in *Mesosuchus*, this contact in *Howesia* is restricted to less than half of the lunate process.

The anterolateral row of palatal denticles on the pterygoid continues on to the palatine for only a short distance. Palatine and ectopterygoid are separated along the medial edge of the suborbital fenestra by a wide entrance of the pterygoid.

Quadrate. A partial left quadrate remains in SAM 5885 (Text-fig. 3A). The quadrate of *Howesia* is a robust bone with a pronounced posterior emargination, a broad union with the quadrate ramus of the pterygoid, and an apparently equally broad lateral exposure that met the quadratojugal. The strongly emarginated quadrate places the craniomandibular joint posterior to the occipital condyle. *Mesosuchus* has a quadrate with similar proportions.

Epipterygoid. A right epipterygoid is exposed in lateral view in SAM 5885 (Text-fig. 3B). It has an expanded, ventrally convex base that rests on the dorsal edge of the quadrate ramus of the pterygoid and a tapering dorsal process (Text-fig. 1C). No significant differences exist between the epipterygoids of *Howesia* and *Mesosuchus*.

Braincase. SAM 5885 has a largely complete and well preserved braincase (Text-fig. 3B). There is no evidence of an archosauriform laterosphenoid (Clark *et al.* 1993). The supraoccipital is transversely broad with a slight, median elevation that separates laterally placed, shallow concavities. Its dorsal margin is straight and does not match the strongly curved occipital rim of the parietals, which indicates that the contact between supraoccipital and parietal is displaced anteriorly on to the ventral side of the parietal. The dorsal corners have small facets for articulation with the parietals. Laterally, the supraoccipital has a broad contact with the prootic and opisthotic. Facets along the foramen magnum received the exoccipitals. As these facets do not merge dorsally, it is clear that the supraoccipital enters the foramen magnum. *Howesia* and *Mesosuchus* share similar plate-like supraoccipitals that are different from the inverted V-shaped supraoccipitals of Middle and Late Triassic rhynchosaurs.

The triangular plate of the parasphenoid has a pair of large, ventrolateral processes next to its transverse suture with the basioccipital. At the base of the basipterygoid processes are a pair of foramina for the cerebral branches of the internal carotid arteries. The basipterygoid processes are stout, project anterolaterally, and expand distally at their joint with the basal processes of the pterygoid. A groove at the base of each basipterygoid process, anterior to the internal carotid foramina, is probably the vidian sulcus which held the vidian nerve (palatine ramus of cranial nerve VII) and the palatine branch of the internal carotid artery. A thin, dorsoventrally tall cultriform process extends anteriorly for a distance at least equal to the length of the parasphenoidal plate.

The basioccipital forms an occipital condyle that appears to be concave on its posterior surface as a result of poor preservation. It does not appear to enter the metotic foramen because the opisthotic and exoccipital join ventrally.

A left exoccipital lies next to the opisthotic on SAM 5885 (Text-fig. 3A). It has a slender middle region which expands dorsally. Ventrally, a pair of foramina for cranial nerve XII (hypoglossal) lie posterior to the metotic foramen.

The left prootic lies against the parietal wing so that only the dorsal half is exposed to reveal its contacts with the opisthotic and supraoccipital (Text-fig. 3A). The configuration of its articulation with the basisphenoid and the existence of a pila antotica and crista prootica, all argued to be synapomorphies of archosauromorphs minus choristoderes (Evans 1990), are unknown.

The left opisthotic has an expanded base where it joins the supraoccipital and prootic. A long, laterally compressed paroccipital process has a slightly enlarged distal end with a blunt face that possibly reached the side of the occiput. The large metotic foramen for cranial nerves IX, X, and XI (glossopharyngeal, vagus, and accessory) and the posterior cerebral vein is formed by the opisthotic and exoccipital. Anterior to the metotic foramen, the opisthotic comprises the posterior border for the fenestra ovalis. A deep fossa extends along the ventral side of the opisthotic from the fenestra ovalis towards the distal end.

Lower Jaw. Little of the mandibles is preserved. SAM 5884 has only the posterior halves of the mandibles (Text-fig. 2), most of which is impression, but this specimen furnishes most information on mandibular sutures.

Only a partial left surangular is present on SAM 5885 (Text-fig. 3). A tiny portion of the dentary, preserved as impression only, is visible on SAM 5884. It evidently tapered to a blunt point between the coronoid and surangular. The coronoid is small and similar to the coronoid of *Mesosuchus* in that it lacks the prominence found in other rhynchosaurs. This prominence on the coronoid is a peak at the level of maximum depth beyond which the profile of the dorsal mandibular margin is slightly concave (e.g. *Hyperodapedon*: Chatterjee 1974). The dorsal margins of the surangulars of *Howesia* and *Mesosuchus* are convex rather than directed posteroventrally as in all other rhynchosaurs. There is no angular preserved, but its impression suggests that it had limited lateral and medial exposures. Virtually the entire inner wall of the adductor chamber is made of the prearticular which expands medially under the articular. SAM 5885 has a partial retroarticular process formed by the articular that is identical to the retroarticular process of *Mesosuchus*. The retroarticular process is robust with a curved posterior margin.

Hyoid. Broom (1906) described a pair of elongate bones lying on the palate of SAM 5884 that he interpreted as hyoid elements. These bones are no longer present and were removed apparently by a previous preparator to allow the complete exposure of the palate. Three fragments of elongate, robust bones are scattered among the palatal elements of SAM 5885 (Text-fig. 3) and evidently are the remains of hyoid bones.

Dentition. *Howesia* shares with Middle and Late Triassic rhynchosaurs the presence of multiple rows of maxillary and dentary teeth. However, in contrast to the later rhynchosaurs with their precision-shear bite where a ridge of dentary teeth cut in to a groove on the maxilla (Benton 1984), the maxillary and dentary teeth of *Howesia* met along a broad occlusal surface as in captorhinid reptiles such as the Early Permian *Captorhinus aguti* (Ricqlès and Bolt 1983).

Portions of the right and left maxillary teeth, an impression of several right dentary teeth, and three left dentary teeth (obscured by the left mandible) are present in SAM 5884 (Text-fig. 2B). A pair of fragments of the left maxilla are separate from SAM 5885 (Text-figs 4A–D, 5). The medially expanded maxilla of *Howesia*
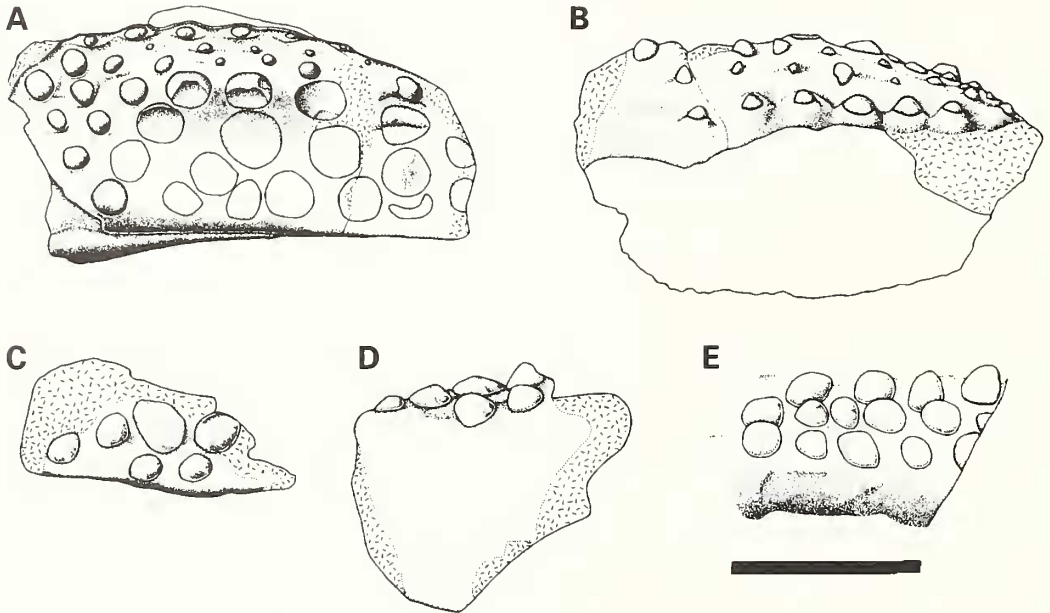

TEXT-FIG. 4. Dentition of *Howesia browni* Broom, 1905; Early Triassic; South Africa. A, maxillary tooth plate of SAM 5885 in occlusal view. B, maxillary tooth plate of SAM 5885 in lingual view. C, fragment of maxillary tooth plate of SAM 5885 in occlusal view. D, fragment of maxillary tooth plate of SAM 5885 in labial view. E, right dentary teeth of SAM 5884 in occlusal view. Scale bar represents 5 mm.

has a strongly convex lingual side and a straight labial side. Teeth are inset from the labial margin as in the other rhynchosaurs with expanded maxillaries. The convex occlusal surface is similar to that of later rhynchosaurs, but lacks a groove. Four rows of occlusal teeth and two rows of lingual teeth are present on the right maxilla of SAM 5884, but this distinction between occlusal and lingual teeth is largely artificial, as noted by Benton (1984) for *Stenaulorhynchus*, because the lingual teeth are part of tooth rows that continue anteriorly on to the occlusal surface.

Unworn occlusal maxillary teeth are conical with a broad base and blunt tip. The largest teeth are present anteriorly and display the greatest wear whereas those at the posterior ends of the tooth rows are smaller and show little or no wear. Enamel covers the entire exposed surface of the unworn teeth.

Teeth of the left maxilla of SAM 5885 are more heavily worn than those of SAM 5884 and reveal more clearly the nature of tooth wear (Text-figs 4A, 5A). Labially facing wear facets are present on those teeth along
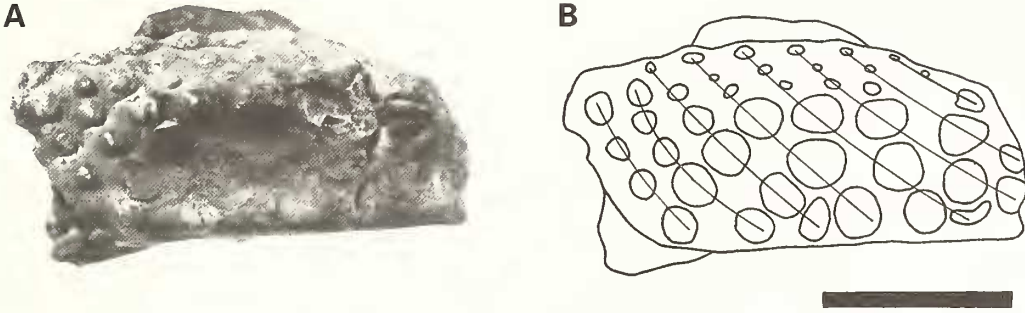
TEXT-FIG. 5. Maxillary tooth plate of *Howesia browni* (SAM 5885) Broom, 1905; Early Triassic; South Africa. A, occlusal view. B, line drawing of A to show Zahnreihen. Scale bar represents 5 mm.

the margin between the occlusal and lingual sides of the maxilla. With the exception of a single unworn tooth at the posterolabial corner, all remaining occlusal teeth are worn down to the level of the maxilla. The pattern of these wear facets indicates that the occlusal teeth met a section of the dentary teeth that is narrower than the width of the maxillary occlusal region. Action of dentary and maxillary teeth apparently initially wore down the teeth to the maxillary surface. Occlusion continued with the dentary teeth wearing against bone to create a broad, shallow depression on the maxilla. Unlike the deep, narrow maxillary grooves of later rhynchosaurs, this depression is not a regular feature of the maxilla because it is absent from the similarly sized maxilla of SAM 5884.

Longitudinal rows of dentary teeth of *Howesia* appear to match the orientation of the rows of maxillary teeth (Text-fig. 4E). The three left dentary teeth of SAM 5884 are damaged. Dentary teeth are conical.

Maxillary and dentary teeth of *Howesia* are implanted deeply in bone (Broom 1906; Malan 1963) as shown by natural breaks. Presumably, bone of attachment anchors the deeply rooted teeth, a form of implantation known as ankylothecodont (Chatterjee 1974; Benton 1984) that is found in rhynchosaurs and probably *Trilophosaurus* (Gregory 1945). Histological sections are needed to confirm this supposition for *Howesia*. Unfortunately, specimens of *Howesia* are too few to justify this sacrifice. Worn maxillary teeth on SAM 5885 show radial dentinal tubules in the dentine and occasional circumferential growth lines. The pulp cavities of these teeth are either largely or completely filled by secondary dentine. Thick secondary bone covers the occlusal and lingual surfaces of the maxilla to such an extent that only the tips of the younger teeth emerge above this bone. Wave-like ridges of secondary bone are present in the posterolingual corner.

The teeth of *Howesia* are arranged in longitudinal or diagonal Zahnreihen (Text-fig. 5B; Edmund 1960; Malan 1963) and apparently share with other rhynchosaurs an identical pattern of ontogenetic addition (Benton 1984). The left maxilla of SAM 5885 shows this pattern most clearly. Patterns of tooth wear, sizes of teeth, and the wave-like nature of the secondary bone suggest that teeth were added during growth to each Zahnreihe at the posterolingual corner of the maxilla on the lingual side. The smallest teeth in the posterolingual corner with only their tips exposed are the youngest. The convexity of the maxilla (Text-fig. 4B) probably separated the younger maxillary and dentary teeth. Older teeth situated more anteriorly in the rows are larger and worn. Growth of the maxilla was presumably by addition of bone posteriorly to provide space for the new teeth. Each wave-like crest of secondary bone could represent successive phases of growth. As each

crest of secondary bone crosses several Zahnreihen, teeth were apparently added simultaneously to the Zahnreihen. Resorption of bone and loss of teeth probably occurred anteriorly.


Axial skeleton

Vertebral column. Of the atlas-axis complex on SAM 5885, only the left atlantal neural arch and the axis are preserved (Text-fig. 3). The atlantal neural arch has the plesiomorphic amniote morphology of a dorsal arm that forms the roof of the neural canal and a posterior arm that forms the postzygapophysis. A lateral ridge on the posterior arm ends at a broken surface, suggesting the former existence of a posteriorly directed spine, a common feature of early amniotes. There is a large, laterally oriented, circular facet for the proatlas at the junction between the two arms of the atlas arch. The axis has an elongate and dorsoventrally low neural spine that extends forward to overhang the atlantal neural arches. Most of the axial neural spine is extremely thin, but it thickens dramatically at the posterior end, possibly for the attachment of the cervical muscle M. spinalis capitus. There is a sharp keel along the ventral margin of the centrum. The anterior one-third of the third cervical vertebrae is in articulation with the axis. The ventral edge of its centrum is rounded gently.

SAM 5886 furnishes all information on the remainder of the postcranium that is known for *Howesia* (Text-figs 6–7). As there is no skull associated with this specimen, the matter of the probable identity of SAM 5886
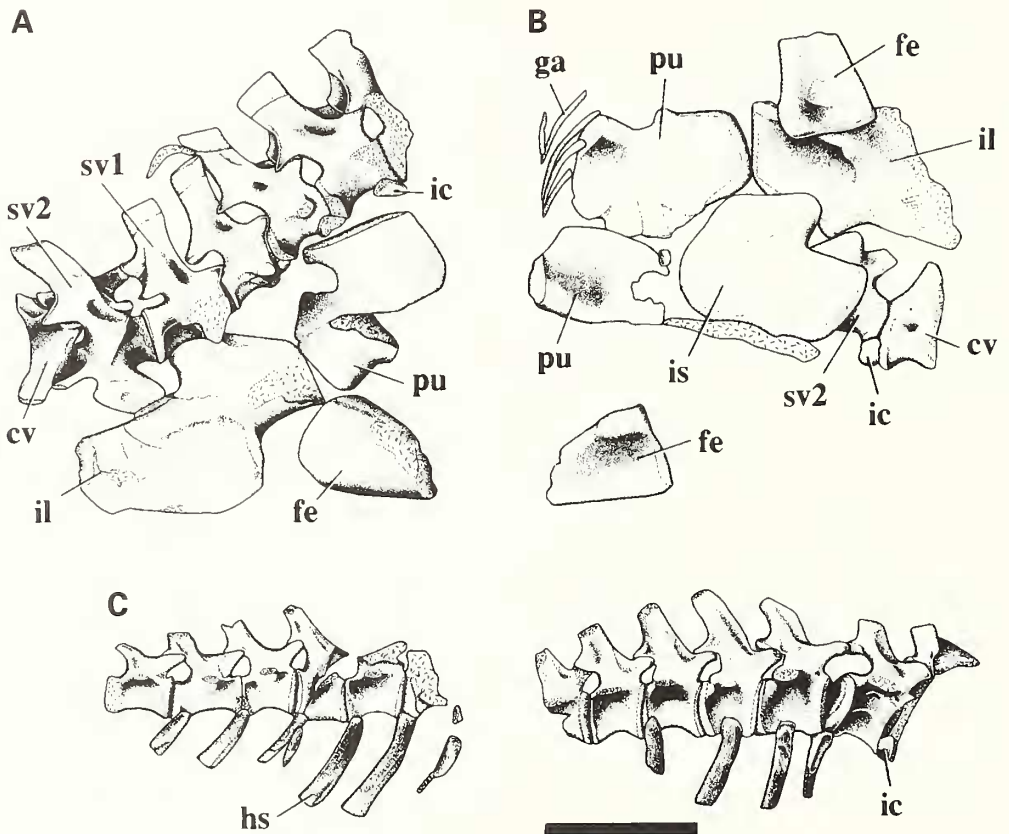
TEXT-FIG. 6. *Howesia browni* Broom, 1905; SAM 5886; Early Triassic; South Africa. A, right dorsolateral view of posterior presacrals, sacrals, first caudal, pelvis, and proximal femur. B, ventral view of pelvis, second sacral, first caudal, and proximal femur. C, right lateral view of articulated caudal vertebrae. Scale bar represents 20 mm.
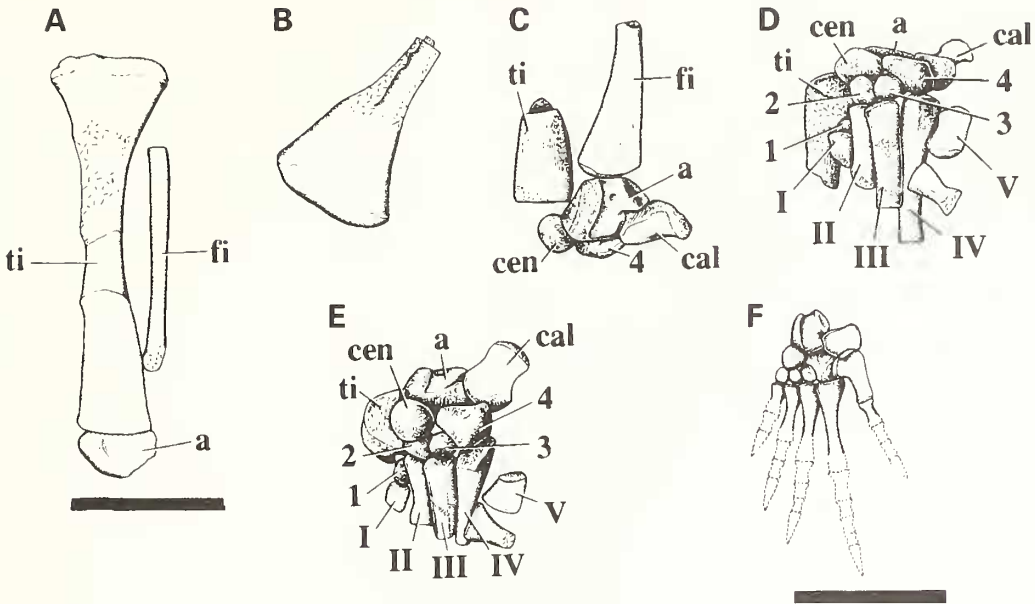
TEXT-FIG. 7. *Howesia browni* Broom, 1905; SAM 5886; Early Triassic; South Africa. A, left tibia, partial fibula, and astragalus in anterior view. B, distal end of left femur in ventral view. C, right pes in posterior view. D, right pes in posteroventral view. E, right pes in ventral view. F, restoration of right pes. Scale bars: A–E (below A) represent 20 mm, F represents 40 mm.

must be addressed first. Broom (1906) argued that SAM 5886 did belong to *Howesia*, and cited as evidence the presence of SAM 5886 in the same horizon as the two partial skulls and an accordance between the morphologies of the pelvis of SAM 5886 and the skull and pectoral girdle of *Howesia*. Neither argument is convincing since both presuppose the non-existence of other vertebrates with similar postcranial morphology. However, there is excellent agreement in general morphology between SAM 5886 and the postcranium of *Mesosuchus*, in particular the pelvis, bifurcate second sacral rib, and tarsus. *Prolacerta* shares these postcranial features with basal rhynchosaurs, but can be distinguished by its narrower, ventrally concave second sacral rib and a tibia that is markedly elongate relative to the femur (Gow 1975). As these features are lacking in SAM 5886, it is likely that this specimen is part of a rhynchosaur. Despite the large number of similarities between SAM 5886 and *Mesosuchus*, there are several differences which indicate that SAM 5886 is not *Mesosuchus* and, indirectly, support assignment of SAM 5886 to *Howesia*, the only other known rhynchosaur from the *Cynognathus* Assemblage Zone. These differences are: the presence of deep pockets on the neural arches of the posterior dorsals and sacrals of SAM 5886 that are absent in *Mesosuchus*; a posterior inclination of the caudal neural spines of SAM 5886 whereas those of *Mesosuchus* are essentially vertical; and the absence on SAM 5886 of a prominent ventral groove on each of the first two caudal centra that is present on *Mesosuchus*. SAM 5886 will, thus, be assigned to *Howesia*, but with the reservation that future discoveries of additional specimens are needed for confirmation.

The posterior four presacrals of SAM 5886 have non-notochordal centra with gently rounded ventral edges (Text-fig. 6). Transverse processes are robust, project significantly beyond the centra, and are directed primarily ventrolaterally and slightly anteriorly. Zygapophyseal surfaces of successive vertebrae meet at an angle of approximately 10° to the frontal plane. A deep pocket is present on the neural arches. Neural spines are tall, and there is no evidence of variation in their height.

Howesia has two sacral vertebrae. Construction of the centra, the angulation of the zygapophyses, and shape of the neural spines differ little from the posterior presacrals. The pockets on the sacral neural arches are larger than those on the dorsals.

Length of the tail of *Howesia* is unknown. Caudal centra change little in length along the preserved string of twelve of SAM 5886 (Text-fig. 6) indicating a very long tail of approximately 50 vertebrae as suggested for

Noteosuchus (Carroll 1976). *Mesosuchus* probably has a tail of similar length. Later rhynchosaurs have shorter tails composed of between 25 and 30 vertebrae (Huene 1938, 1942; Benton 1983*b*, 1990). A pronounced transverse narrowing of the tail is shown by a significant decrease in the width of the centra past the sixth caudal. The first caudal vertebra has an elongate, blade-like transverse process that projects posterolaterally; all succeeding caudal transverse processes are broken, but it is clear that those past the third caudal project only laterally. Each caudal centrum has a rounded ventral edge that is characterized on vertebrae six to twelve by a sharp, central ridge and flanking, secondary ridges. Shallow depressions on the neural arches that disappear by the ninth caudal are all that remain of the deep pockets on the sacrals and dorsals. There is no apparent change in the angulation of the caudal zygapophyses relative to the dorsals. Neural spines are tall, but much narrower than those of the dorsals, and incline progressively more posteriorly on distal caudals. The caudal neural spines of *Mesosuchus* and *Rhynchosaurus* (Benton 1990) are equally tall, but those of the proximal caudals are vertical in both genera.

Crescentic intercentra are present along the preserved section of dorsals and the proximal two caudals. Haemal arches are elongate with a distal expansion that is greater than at the proximal end. Faint striations cover the haemal arches. The tall neural spines and long haemal spines give the tail of *Howesia* a very deep lateral profile.

Ribs. A single cervical rib has an expanded, apparently holocephalous head and a slender shaft (Text-fig. 3A). Both pairs of sacral ribs are fused to the centra (Text-fig. 6A). Only the base of the right first sacral rib is exposed, but it indicates a very robust rib that probably had a firm union with the pelvic girdle. The bifurcate second sacral rib has a greatly enlarged anterior division with a distally expanded, elliptical articular end and a much smaller, blade-like posterior division that does not reach the pelvic girdle.

Gastralia. Five posterior gastralia are preserved along the anterior edge of the left pubis (Text-fig. 6B). Each is very thin and narrows towards the body midline.

Appendicular skeleton

Pectoral girdle and forelimb. Broom (1906) described and figured a partial shoulder girdle and humerus for SAM 5885. However, these elements are not now present with SAM 5885 nor could they be found in the collections of the South African Museum. It is presumed that they are lost. As illustrated (Broom 1906, pl. 40, fig. 10), the scapula narrows dramatically above the glenoid unlike the much broader scapula of *Mesosuchus*. However, Broom noted that the anterior margin was incomplete, and the narrow scapular configuration is probably an artefact.

Pelvic girdle. Each element of the pelvic girdle is enlarged and plate-like with the ilium making the greatest contribution to the acetabulum (Text-fig. 6B). The ilium is very similar to that of *Mesosuchus* and *Noteosuchus* (Carroll 1976) in having a constriction above the acetabulum and a dorsally expanded blade with a larger, posterior expansion. Later rhynchosaurs, with the exception of *Rhynchosaurus* (Benton 1990), have equally developed anterior and posterior extensions of the ilium. Facets for reception of the paired sacral ribs are present on the medial side of the ilium. The facet for the first sacral rib appears larger, and is bounded anteriorly, ventrally and posteriorly by ridges. The facet for the second sacral rib is posterodorsally elongate with an expanded ventral margin which matches the shape of the rib's articular end.

The pubis of *Howesia* is identical to that of *Mesosuchus*, *Noteosuchus* and *Prolacerta* in its possession of a transversely broad, down-turned anterior region and a prominent, ventrally pointing processus lateralis. A large, elliptical obturator foramen is situated near the lateral edge at the level of the downward curvature. The pubes meet medially for most of their lengths, but diverge close to the ischia to border a large, diamond-shaped opening.

The ischium is a posteriorly curved, flat bone. There are few differences between the ischia of *Howesia* and other rhynchosaurs.

Hindlimb. As with the pelvic girdle, bones of the hindlimb of *Howesia* are virtually identical to those of the other two Early Triassic rhynchosaurs. Neither femur of SAM 5886 is complete; the left consists of the ends and a portion of the intervening shaft (Text-figs 6B, 7B). Matching the ends to the shaft can give only an

imprecise estimate of femoral length, but it is clear that the femur and tibia were approximately equal in length. Proximally, the articular surface is flat and continuous with the large internal trochanter. There is a slight sigmoidal curvature to the shaft. The distal condyles have only a modest convexity and are equal in size.

The tibia has a broad proximal platform and no cnemial crest (Text-fig. 7A). The shaft is narrowest in the middle and expands slightly at the distal end. The fibula has a narrow shaft and a flattened distal end that is equal in width to the distal end of the tibia.

Terminology for the tarsus (Text-fig. 7C–E) follows Carroll (1976) rather than Hughes (1968) and Chatterjee (1974). The proximal end of the hooked fifth metatarsal, illustrated by Carroll (1976, fig. 8), is absent and could not be found in the collections of the South African Museum. The calcaneum has a prominent, laterally directed tuber with an expanded, blunt end. The astragalus has a large, lateral peg that contacts the fibula, and a deep notch immediately below this peg is the medial border of a perforating foramen. As restored by Carroll (1976, fig. 8), three proximal tarsals, the calcaneum, astragalus, and centrale, form a row along the bottom of the crus. However, it is clear that the entire lateral side of the astragalus received the tibia and the centrale should be positioned against the distal side of the astragalus. Consequently, *Howesia* retains the plesiomorphic amniote configuration of only two proximal tarsals, the astragalus and calcaneum (Text-fig. 7F). Four distal tarsals are present. Distal tarsals one to three are smaller than the fourth, and articulate with the entire proximal ends of their respective metatarsals. The centrale and the fourth distal tarsal contact in *Howesia* and *Mesosuchus*. Carroll's restoration of the pes of *Noteosuchus* (Carroll 1976, fig. 6C) has the correct arrangement of tarsals for an Early Triassic rhynchosaur. The first four metatarsals are expanded and overlap proximally. The fifth metatarsal is hooked, but as the proximal half is now missing from SAM 5886, nothing can be added to the description of Carroll (1976).

PHYLOGENETIC RELATIONSHIPS

There has been no disagreement in the literature that the Middle and Late Triassic rhynchosaurs form a natural group. With their robust skulls, huge batteries of maxillary teeth, deep lower jaws and toothless beak, these rhynchosaurs are clearly different from any other known reptile. Instead, discussion has centred upon the phylogenetic relationship of the Early Triassic genera to the later 'typical' rhynchosaurs. Broom (1906) recognized close affinities between *Howesia* and the rhynchosaurs *Rhynchosaurus* and *Hyperodapedon* primarily on the basis of their extremely similar dentition, but the possibility of a close relationship between *Howesia* and *Mesosuchus* and the pseudosuchians, the grade of unspecialized thecodonts considered to be ancestral to a variety of archosaurs such as dinosaurs and birds, was soon suggested (Broom 1913). In a classification of early tetrapods (Watson 1917), the thecodontian family Howesiidae was erected to include *Howesia*, *Mesosuchus* and *Proterosuchus*, and the remaining rhynchosaurs were placed as a separate family of rhynchocephalians.

This proposal of a thecodontian ancestry for *Howesia* does not appear to have gained many proponents and was soon forgotten. Instead, it was accepted for many years that the Middle and Late Triassic rhynchosaurs form a group separate from the earlier genera and that *Howesia* with its multiple rows of maxillary teeth lay at the base of their radiation (Huene 1939a, 1939b; Malan 1963; Kuhn 1969; Sill 1970; Chatterjee 1980). Cladistic analyses (Benton 1985, 1987, 1990; Evans 1988) have positioned *Howesia* as the sister taxon to the later rhynchosaurs. However, given the inadequate information in the literature, *Howesia* could play only a minor role in phylogenetic analyses of Rhynchosauria despite its apparent significance. For the first time, there is now sufficient data available for a more rigorous evaluation of the phylogenetic position of *Howesia* within Rhynchosauria.

Only the better known rhynchosaur taxa, *Mesosuchus*, *Howesia*, *Rhynchosaurus articeps*, *Stenaulorhynchus*, *Scaphonyx* and *Hyperodapedon*, are included. Three outgroups were selected from the diversity of known basal archosauromorphs: *Champsosaurus* (Russell 1956; Erickson 1972), *Trilophosaurus* (Gregory 1945), and *Prolacerta* (Gow 1975). Although the relationships of choristoderes such as *Champsosaurus* are uncertain, the taxon is a member of Archosauromorpha (Gauthier 1984; Rieppel 1993). Only a single archosauromorph, *Prolacerta*, was used in the study of Benton (1990); the remainder (*Petrolacosaurus*, *Claudiosaurus*, *Thadeosaurus* and *Youngina*) are distantly related basal diapsids that are too far removed phylogenetically for a most parsimonious
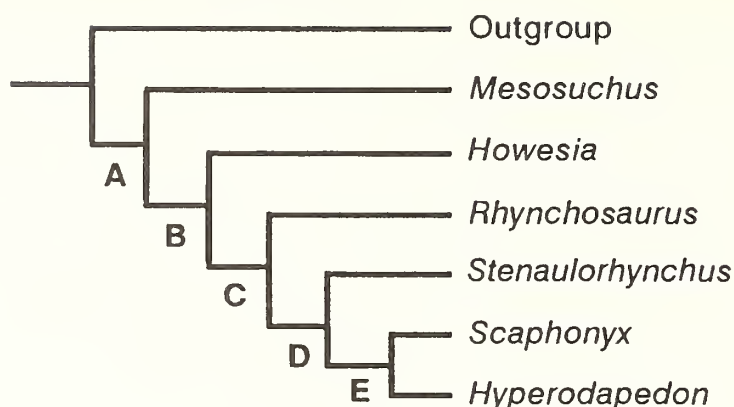
TEXT-FIG. 8. Cladogram depicting hypothesis of interrelationships of Rhynchosauria. Polarity of character states was determined through outgroup analysis of *Champsosaurus*, *Trilophosaurus*, and *Prolacerta*, and a hypothetical ancestor constructed to root the tree. Nodes are diagnosed by the following unambiguous characters: A, (Rhynchosauria), beak-shaped premaxilla, single median external naris, contact present between premaxilla and prefrontal, depression on dorsal surface of frontal, depression on dorsal surface of postfrontal, fused parietals, flat occlusion. B, maxilla with convex occlusal margin, absence of anterior process of nasal projecting in to external naris, presence of maxillary tooth plate, ankylothecodont tooth implantation, maxillary teeth on occlusal and lingual surfaces. C, ratio of lengths of frontal and parietal $\leqslant 1\cdot0$, presence of lateral shelf on jugal, absence of palatal teeth on pterygoid, contact between ectopterygoid and palatine to exclude maxilla from suborbital fenestra, a row of three proximal tarsals (astragalus, calcaneum, and centrale), blade and groove occlusion, two grooves on maxilla. D, basipterygoid articulation is posterior to transverse flange of pterygoid, equally large anterior and posterior processes of ilium, ratio of distal femoral width and total femoral length $> 0\cdot3$. E, midline skull length greater than maximum skull width, robust subtemporal process of jugal with its height > 50 per cent. of its length, single groove on maxilla, depth of lower jaw at adductor fossa > 25 per cent. of total jaw length, maxillary teeth only on occlusal surface, absence of posterior process on coracoid, absence of postaxial intercentra.

determination of the plesiomorphic characters for Rhynchosauria according to Rule 3 of Maddison *et al.* (1984). The present phylogenetic study should be considered preliminary pending the completion of a redescription of *Mesosuchus*.

The data matrix used this study (Appendix 2) is based upon the matrix given in the latest phylogenetic analysis of Rhynchosauria (Benton 1990). The following characters (identified by the same numbering sequence as in Benton (1990) with the prefix B to denote their source) are retained from this data matrix with no modification: B1, B4, B7, B8, B13, B15, B16, B18, B20, B21, B23, B25. Those characters of Benton (1990) included in this analysis with modification and those excluded are discussed in Appendix 3.

A total of 28 characters were used in this study. They were analysed with the program Hennig86 (Farris 1988). All characters were run unordered, and the most parsimonious tree calculated by the implicit enumeration (ie) command.

A single most parsimonious tree (Text-fig. 8) was obtained. It has a length of 32 steps and consistency and retention indices of 0·93. The tree is extremely similar to that of Benton (1990) with the exception of a reversal of the positions of *Rhynchosaurus* and *Stenaulorhynchus*. The explanation for this reversal is found in character B14, the only character that supported the node of *Rhynchosaurus* + *Scaphonyx* + *Hyperodapedon* in Benton (1990). With the polarity of this character corrected in the present analysis, the derived state failed to support a node because it is found in only *Mesosuchus* and *Stenaulorhynchus* and is unknown for *Howesia*.

Seven synapomorphies diagnose Rhynchosauria: (1) a beak-shaped premaxilla; (2) a single, median external naris; (3) contact between the premaxilla and prefrontal; (4) depression on the

dorsal surface of the frontal; (5) depression on the dorsal surface of the postfrontal; (6) fused parietals; and (7) flat jaw occlusion. Discovery of a single, median external naris in *Howesia* confirms previous suggestions that this character is a synapomorphy of rhynchosaurs (Chatterjee 1980; Benton 1985, 1987, 1990; Evans 1988). The only other group of basal diapsids that has a single external naris is the choristoderes, e.g. *Champsosaurus* (Erickson 1972). Characters 3–5 are proposed as new synapomorphies for rhynchosaurs. A contact between the premaxilla and prefrontal is apparently unique to rhynchosaurs among early diapsids although this character state is unknown for *Trilophosaurus* (Gregory 1945). A new burrowing saurian diapsid from the Jurassic of Mexico (Clark and Hernandez 1994) may also have a contact between the premaxilla and prefrontal, but the identification of the prefrontal is uncertain. Depressions are present on the dorsal surfaces of the frontals and postfrontals for all rhynchosaurs, with the possible exception of *Rhynchosaurus* (Benton 1990). *Champsosaurus* appears to have a depression on the postfrontal (Russell 1956; Erickson 1972), but a depression is absent on the postfrontal of the basal choristodere *Cteniogenys* (Evans 1990). Fusion of parietals has been proposed as a synapomorphy of rhynchosaurs (Chatterjee 1980; Benton 1985). Flat jaw occlusion where maxillary and dentary teeth meet along a broad occlusal surface was not recognized as a rhynchosaurian synapomorphy by Benton (1990) because the character was not separated from the plesiomorphic character state of lateral overlap of maxillary teeth against dentary teeth.

Additional characters that have been proposed as synapomorphies of rhynchosaurs appear to diagnose more inclusive or more restrictive clades than Rhynchosauria. A row of three proximal tarsals (Benton 1985, 1987, 1990; Evans 1988) is a synapomorphy of only the Middle and Late Triassic rhynchosaurs because *Howesia*, *Mesosuchus*, and *Noteosuchus* share the plesiomorphic character of only two (astragalus and calcaneum) proximal tarsals. An anterior position of the occipital condyle relative to the craniomandibular joint (Benton 1990) could diagnose a more inclusive clade than Rhynchosauria because this character is also present in *Prolacerta* (contrary to Gow 1975) and archosauriforms such as *Proterosuchus* (Cruickshank 1972) and *Euparkeria* (Ewer 1965). Evans (1988) added the characters of cervical centra that are shorter than dorsal centra and phalanges that are short in relation to the metapodials. The first character is probably plesiomorphic for diapsids (Laurin 1991) and is not correct for *Mesosuchus*. The second character is not quantified, and appears to be correct only for the Middle and Late Triassic rhynchosaurs.

As concluded in previous phylogenetic studies, *Howesia* is most closely related to the clade of the Middle and Late Triassic genera (Text-fig. 8). *Howesia* shares with these rhynchosaurs five synapomorphies that are primarily of the dentition. Three of these synapomorphies supported the same clade in Benton (1990): ankylothecodont tooth implantation, presence of a maxillary tooth plate (i.e. batteries of teeth), and maxillary teeth on occlusal and lingual surfaces. The remaining pair of unambiguous synapomorphies of this clade in Benton (1990) (frontal shorter than parietal and presence of parietal foramen) fail to support the clade in the present study because the first character is a synapomorphy of only the Middle and Late Triassic genera and the second character is excluded for the reason given in Appendix 3. Two new synapomorphies of *Howesia* and later rhynchosaurs are a maxilla with a convex occlusal margin and the absence of anterior processes of the nasals that project into the external naris. Plesiomorphically, the maxilla of diapsids has a straight occlusal margin whereas *Howesia* (Text-fig. 4B) and later rhynchosaurs have a distinctly convex occlusal margin. *Mesosuchus* retains the plesiomorphic character of narrow anterior processes of the nasals (Haughton 1924) which in other diapsids contact anterodorsal processes of the premaxillae to separate the external nares. These processes of the nasals are absent in *Howesia* and later rhynchosaurs.

in making the latex peels of SAM 5884. Comments on the manuscript from Drs Bruce Rubidge, Michael Benton, and Andrew Milner are greatly appreciated.

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APPENDIX 1 – ABBREVIATIONS USED IN THE TEXT-FIGURES

a	astragalus	mtp	maxillary tooth plate
aa	atlas neutral arch	n	nasal
ar	articular	op	opisthotic
ax	axis	p	parietal
bo	basioccipital	pal	palatine
cal	calcaneum	pf	postfrontal
cen	centrale	pm	premaxilla
co	coronoid	po	postorbital
cr	cervical rib	pra	prearticular
ct	cultriform process	prf	prefrontal
cv	caudal vertebra	pro	prootic
d	dentary	ps	parasphenoid
ect	ectopterygoid	pt	pterygoid
eo	exoccipital	pu	pubis
ept	epipterygoid	q	quadrate
ga	gastralia	qj	quadratojugal
f	frontal	rtp	retroarticular process
fe	femur	s.l	suture for lacrimal
fi	fibula	s.m	suture for maxilla
h	hyoid	s.pm	suture for premaxilla
hs	haemal spine	s.po	suture for postorbital
ic	intercentrum	sa	surangular
ica	foramen for internal carotid artery	sc	sclerotic plates
		so	supraoccipital
idt	impression of dentary teeth	sq	squamosal
		sv1	sacral vertebra 1
il	ilium	sv2	sacral vertebra 2
is	ischium	st	supratemporal
j	jugal	ti	tibia
l	lacrimal	v	vomer
m	maxilla	1–4	distal tarsals 1–4
mptsh	medial pterygoid shelf	I–V	metatarsals 1–5

APPENDIX 2

Description of the characters used in the phylogenetic analysis. The plesiomorphic state is denoted by 0 and derived states by 1 and 2. Characters were polarized using *Champsosaurus*, *Trilophosaurus*, and *Prolacerta* as outgroups.

1. Dimensions of skull: midline length > maximum width (0); midline length < maximum width (1).
2. Premaxilla and anterior part of dentary: teeth present (0); edentulous (1).
3. Shape of premaxilla: horizontal ventral margin (0); beak-shaped (1).
4. External nares: separate (0); single, median naris (1).
5. Premaxilla and prefrontal: no contact (0); contact present (1).
6. Maxilla: horizontal ventral margin (0); convex ventral margin (1).
7. Location of maxillary teeth: only on occlusal surface (0); occlusal and lingual surfaces (1).
8. Maxillary tooth plate: absent (0); present (1).
9. Number of grooves on maxilla: none (0); one (1); two (2).
10. Jaw occlusion: single-sided overlap (0); flat occlusion (1); blade and groove (2).
11. Tooth implantation: subthecodont (0); ankylothecodont (1).
12. Anterior process of nasals: present and project into external naris (0); absent (1).
13. Ratio of lengths of frontals and parietals: > 1·0 (0); ≤ 1·0 (1).
14. Depression on dorsal surface of frontal: absent (0); present and next to sutures with postfrontal and parietal (1).
15. Depression on dorsal surface of postfrontal: absent (0); present (1).
16. Fusion of parietals: absent (0); present (1).
17. Lateral shelf on jugal above maxillary teeth: absent (0); present (1).
18. Subtemporal process of jugal: robust with height > 50 per cent. of length (0); slender with height < 50 per cent. of length (1).
19. Teeth on palatal ramus of pterygoid: present (0); absent (1).
20. Suborbital fenestra: ectopterygoid and palatine do not contact along lateral margin of fenestra (0); ectopterygoid and palatine contact to exclude maxilla from fenestra (1).
21. Location of basipterygoid articulation relative to transverse flange: coincident with flange (0); posterior to flange (1).
22. Depth of lower jaw measured at maximum height of adductor fossa relative in total length of lower jaw: < 25 per cent. (0); > 25 per cent. (1).
23. Ratio of lengths of dentary and lower jaw: > 0·5 (0); ≤ 0·5 (1).
24. Posterior process on the coracoid: present (0); absent (1).
25. Dorsal margin of ilium: small anterior process and larger posterior process (0); equally large anterior and posterior processes (1).
26. Ratio of distal width of femur and total femoral length: ≤ 0·3 (0); > 0·3 (1).
27. Number of proximal tarsals: two (astragalus and calcaneum) (0); three (astragalus, calcaneum, and centrale) (1).
28. Postaxial intercentra: present (0); absent (1).

APPENDIX 3

Characters of Benton (1990) included with modification:

B2. Premaxillary teeth: present (0); reduced numbers or absent (1). As the number of premaxillary teeth is unknown for *Howesia*, their reduction in number may be autapomorphic for *Mesosuchus*. Instead, this character is modified to the presence or absence of premaxillary teeth.

B3. Premaxillary shape: straight lower edge, with teeth (0); beak-shaped and toothless (1). The existence of premaxillary teeth and the shape of the premaxilla are separate characters because they do not necessarily occur together in diapsids. For example, *Mesosuchus* has a beak-shaped premaxilla with teeth whereas the outgroup *Trilophosaurus* has a straight-edged premaxilla that lacks teeth. Therefore, this character is reworded to describe only the shape of the premaxilla.

B5. Jugal size: smaller than maxilla (0); larger than maxilla and occupies a large area of the cheek (1). This character is difficult to quantify because it is not stated in which dimensions the jugal and maxilla are to be compared. The robustness of the jugal is expressed instead as a measure of the relative dimensions of the subtemporal process.

B14. Relative length of the dentary: half, or less than half the total length of the lower jaw (0); well over half the total length of the lower jaw (1). Outgroup analysis shows that the polarity of this character should be reversed. A dentary that is greater than half of the total length of the mandible is plesiomorphic for Rhynchosauria.

B17. Jaw occlusion: flat occlusion or single-sided overlap of teeth (0); blade and groove apparatus, where dentary blade(s) fit precisely into maxillary groove(s) (1). The plesiomorphic character state is overlap of teeth during occlusion with flat occlusion and blade and groove occlusion comprising the derived states.

B22. Teeth on the pterygoid: present (0); absent (1). It is uncertain whether this character refers to teeth on both the palatal ramus and transverse flange or only the palatal ramus. It is reworded herein to refer to only the palatal ramus of the pterygoid.

Characters of Benton (1990) excluded from analysis:

B6. Frontal shape: longer than broad (0); broader than long (1). The derived character state is autapomorphic for *Stenaulorhynchus* and is, therefore, excluded.

B9. Parietal foramen: present (0); absent (1). Absence of a parietal foramen is plesiomorphic for rhynchosaurs because it is absent in the outgroups *Trilophosaurus* and *Champsosaurus*, polymorphic for *Prolacerta* (Gow 1975; personal observation), and absent in the basal archosauriforms *Euparkeria* and *Proterosuchus* (personal observation). The presence of a parietal foramen is apparently autapomorphic for *Mesosuchus*.

B10. Supratemporal: present (0); absent (1). This character is excluded because it is uncertain for *Stenaulorhynchus* (Benton 1990) and there is discrepancy in the literature as to whether this bone is absent (Huene 1942) or present (Sill 1970) in *Scaphonyx*.

B11. Shape of the ventral process of the squamosal: narrow and strap-like (0); broad and plate-like (1). This character is not quantified and cannot be determined for the outgroups *Trilophosaurus* and *Champsosaurus*.

B12. Relative position of occipital condyle: approximately in line with the quadrates (0); well in front of the quadrates (1). This character cannot be polarized by outgroup analysis because *Champsosaurus* and *Trilophosaurus* have a third character state of an occipital condyle that is posterior to the quadrates and *Prolacerta* has the supposedly derived state of the occipital condyle anterior to the quadrates. It is necessary to examine the distribution of this character in a broader study of archosauromorphs.

B19. Maximum width of the tooth-bearing areas of the maxilla lying lateral to the main groove: narrower than the medial area (0); equal in width to, or wider than, the medial area (1). It is impossible to code this character for the outgroups, *Mesosuchus*, and *Howesia* because they lack a maxillary groove.

B24. Relative length of the femur and humerus: femur is longer than the humerus (0); humerus is longer than the femur (1). Only *Hyperodapedon* has the derived character state.

B26. Relative size of the centrale: small (0); large, and closely associated with the astragalus (1). The size of the centrale is not quantified, and the distribution of this character becomes identical to that of B25 following correction of the number of proximal tarsals in *Howesia* and *Mesosuchus*.

APPENDIX 4

Data matrix used in phylogenetic analysis. Numbers (1–28) at the top of each column refer to the characters listed in Appendix 2. A question mark indicates an unknown character state.

Character

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Champsosaurus	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Trilophosaurus	0	1	0	0	?	0	0	0	0	1	1	0	0	0
Prolacerta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosuchus	0	0	1	1	1	0	0	0	0	1	0	0	0	1
Howesia	?	?	?	1	1	1	1	1	0	1	1	1	0	1
Rhynchosaurus	0	1	1	1	1	1	1	1	2	2	1	1	1	?
Stenaulorhynchus	0	1	1	1	1	1	1	1	2	2	1	1	1	1
Scaphonyx	1	1	1	1	1	1	0	1	1	2	1	1	1	1
Hyperodapedon	1	1	1	1	1	1	0	1	1	2	1	1	1	1

Character

Taxon	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Champsosaurus	1	0	0	0	0	0	1	0	0	0	0	0	0	1
Trilophosaurus	0	0	0	?	1	0	0	0	0	0	0	0	0	0
Prolacerta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosuchus	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Howesia	1	1	0	0	0	0	0	?	?	?	0	?	0	0
Rhynchosaurus	?	1	1	0	1	1	0	0	0	0	0	0	1	?
Stenaulorhynchus	1	1	1	0	?	1	1	0	1	0	1	1	1	0
Scaphonyx	1	1	1	1	1	1	1	1	0	1	1	1	1	1
Hyperodapedon	1	1	1	1	1	1	1	1	0	1	1	1	1	1